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BIOLOGY AND ECOLOGY OF THE LODGEPOLE NEEDLE MINER

Progress Report of Research in 1957

By George R. Struble

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CALIFORNIA FOREST AND RANGE EXPERIMENT STATION
FOREST SERVICE, U.S. DEPARTMENT OF AGRICULTURE

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SUMMARY

Investigations of a serious lodgepole needle miner outbreak in progress in Tuolumne County since 1947 have been under way since 1954. Their purpose is to determine the biotic and ecological factors underlying outbreaks, as a basis for developing control practices. Studies thus far have covered two complete needle miner generations.

Research on the last half of the 1955-1957 generation and the establishment of the 1957-1959 generation is the subject of this progress report. Main events in the needle miner cycle studied were the last larval instar, pupation, emergence, flight, oviposition, and establishment of the young larvae. Data were obtained on the numbers reaching maturity and emergence. Factors were studied which influence the completion of biological events. Comparisons of populations in the same stage of development between the current (1955-1957) and previous generations in specific areas provide some insight into the trend of outbreak populations. The more important points determined are listed below.

1. Maturing populations in all except the oldest infestation areas were higher than any yet recorded; the average number of maturing larvae and pupae in the latest whorl was 27.2. In the oldest infestation areas the needle miner population decreased.

2. The numbers of maturing larvae and pupae in the latest 5 whorls in the heaviest of the new infestation areas was in excess of 60 individuals.

3. Great masses of dead larvae in webs at tree bases and in silken tents over saplings indicated that starvation was a factor in reducing populations in older infestation areas. Some maturing larvae migrated to other hosts and completed their development to the adult stage.

4. Parasitism and wind-dropped, mined foliage containing pupae, contributed to the mortality due to natural factors; the

total amount recorded among maturing broods owing to these two factors was upwards of 35 percent. Parasites most prevalent were polyembryonic Copidosoma spp.

5. At least 12 species of birds were found to feed on or were suspected of feeding on needle miner larvae, pupae, and adults.

6. The moth emergence period, from July 7 to August 10, was earlier than recorded previously. Males outnumbered females during the first 2 weeks, but females predominated later, equalizing the sex ratio.

7. Prevailing air currents during flight strongly influenced the direction and spread of infestations.

8. The first eggs were found July 23 and the maximum number 2 weeks later. The first hatch was August 21, and by September 11 about half the eggs had hatched. Most of the unhatched eggs were by then ready to hatch.

9. The number of newly established larvae of the 1957-1959 generation was sharply reduced in older infestation areas, in comparison with the number established in these same areas in the previous generation.

10. Studies on the effect of needle miner defoliation on the growth increment of surviving trees have revealed sharp and long-sustained declines in growth.

INTRODUCTION

Research on the lodgepole needle miner, Recurvaria milleri Busck has been under way since 1954 in the High Sierra lodgepole pine forests. It was started because of a severe outbreak, first reported in 1947, for which no methods of control were known. Records of two previous outbreaks since 1910 revealed that the combination of high needle miner populations and subsequent epidemic attacks of the mountain pine beetle resulted in "ghost forests." The present outbreak is following a similar course.

The infested stands are located at elevations between 8,000 and 10,000 feet in the upper Tuolumne and immediately adjacent Merced River watersheds in Yosemite National Park, Tuolumne County. When first reported, the current needle miner outbreak covered a few thousand acres of lodgepole pine forests. By 1957 it had spread to upwards of 50,000 acres. All ages and sizes of trees larger than the smallest saplings are affected. The killing of entire stands as a result of this outbreak first became evident in 1953. The killing started in the areas of oldest infestation. Since then extensive areas of dead forest have resulted.

The investigations begun in 1954 undertook to establish and continue year by year records of the needle miner populations in given areas or plots. Biological studies were started to uncover additional information on the life cycle and habits of the insect. Studies were also started on the natural factors contributing to the reduction of populations, such as insect parasites, diseases, and climatic factors. Research was begun on the effect of insecticides and their possible use in suppressing needle miner outbreaks.

Previous research in this same locality by J.E. Patterson (3) and J.S. Yuill (9) disclosed that the lodgepole needle miner has a 2-year life cycle. The insect reaches the adult stage and oviposition occurs every odd-numbered year. It spends the even-numbered years in the larval stage. Off-season broods or flights of moths in even-numbered years are unknown. This fact, of relatively unique entomological significance, has been verified repeatedly in records of the current outbreak.

Studies which have been conducted from 1954 to 1956 served to: (1) provide a better understanding of the development and behavior of the needle miner during a period of two generations; (2) develop sound techniques for determining population numbers and predicting an outbreak; (3) uncover new information on the incidence and importance of natural enemies, especially insect parasites and predators; (4) evaluate some of the effects of ecological factors, especially climate and food supply; (5) determine the killing effectiveness of new toxic spray formulations against larvae and adults. Details of this work have been presented in four separate progress reports (5,6,7,8).

The present report is the fifth in the series. It covers research conducted during the final phases of the 1955-1957 needle miner generation, and the establishment of the 1957-1959 generation. This work was concerned with: (1) the development and use of improved techniques in measuring and evaluating populations; (2) comparisons with preceding generations as a means of establishing outbreak trends; (3) habits of maturing stages, and ecological influences, especially air currents; (4) and finally, information on the effects of defoliation on the host trees.

Field studies in 1957, as in previous years, were conducted at Tuolumne Meadows, Yosemite National Park. Facilities for these studies were provided by the National Park Service. They consisted of tent accommodations for laboratory, lodging, and cooking. Electric lighting, water, shower, and sanitary facilities were provided. A permanent storage-laboratory building was erected in 1957. This building is 12-feet wide by 16-feet long. It serves the dual purpose of equipment storage in winter and research laboratory in summer.

Studies on the incidence of pathogens affecting needle miner populations in 1957 (1) were undertaken through the cooperation of Dr. Mauro E. Martignoni, Department of Biological Control, University of California.

Assistance in 1957 was provided by Walt L. Muhlbach, graduate student in zoology, University of California. In addition to helping on other phases of the study, he contributed valuable information on the identity and role of birds as a factor in the natural control of the needle miner.

MATURING POPULATIONS OF THE 1955-1957 GENERATION

Abundance

Old infestations

In older infestation areas, the 1955-1957 generation was sampled June 10-25, 1957, to determine the amount of needle miner mortality and survival after the second winter. The sampling technique used was the same as that developed previously, which considers only the terminal whorl of foliage in a sufficient number of samples to provide a sampling error of 10 percent or less. In nearly all cases 40 tips taken at midcrown level from 10 trees was sufficient (figure 1). The sample of each tip, as in previous records, consisted of 10 randomly selected needles. The number of needle miners per tip was determined from the mean number per sample in any given area times 6, the full complement of an average tip as determined from numerous records.

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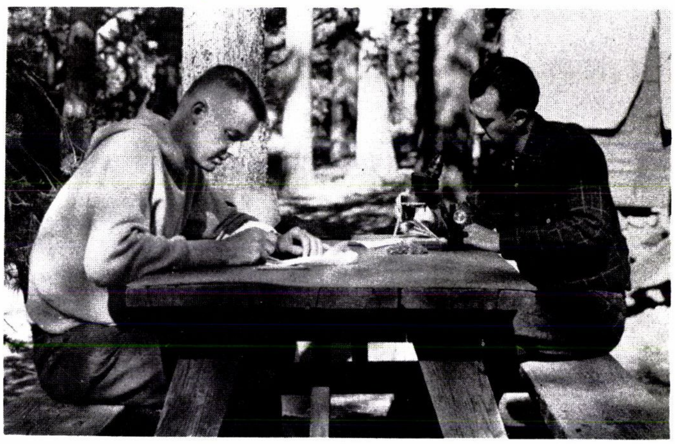

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Figure 1.--Sampling Needle Miner Populations. A, collecting tip samples at midcrown in old infestation area; B, examining needle miner larvae to record living and dead.

The number of fully grown larvae and pupae occurring in different plots and areas after the second winter are recorded in table 1. Populations in all areas were sufficient to cause the complete mortality of the terminal foliage before mid-May 1957. This meant that with the exception of the plot samples and the Conness sample no living foliage was left. In these two exceptions older unmined foliage occurred in varying amounts, especially toward the basal portions of the crowns. Mortality among these populations ranged from 4.2 to 33.6 percent; the average was 16.9 percent. Mortality was attributed both to parasitism and to climatic factors.

Table 1.--Number of needle miners after second winter - 1955-1957 generation

Plot or area	Generations of outbreak numbers	Number of larvae and pupae per tip: Mean		SE	Percent mortality
A	2	31.02	±	2.22	15.9
B	2	43.80	±	2.14	8.6
C	3	34.50	±	2.52	12.5
G	4	38.70	±	2.38	14.7
Conness*	2	20.10	±	1.90	33.6
Dingley	5	21.06	±	2.41	7.2
Delaney	4	24.18	±	2.22	32.3
Cathedral Lake	4	20.40	±	1.84	14.0
Cathedral Creek	4	20.10	±	2.28	24.4
East Cathedral	3	18.00	±	1.76	4.2

* Infestation north of Young Lake which escaped earlier outbreak.

The number of larvae of the 1955-1957 generation surviving the first and second winter is shown in table 2. The data are for plots and areas sampled both in the spring of 1956 and 1957. They reveal two significant points: (1) the increase in number of needle miners in 1957 over 1956 for the plots; and (2) the great reductions during this same period for the other two areas. The increase is due to the migration of larvae to the terminal whorl from foliage further back on the tip. This is characteristic if such foliage is still present, as was the case in all 3 of the plots. The great reductions shown by the Dingley and Cathedral Lake data are the result of abandonment of the terminal whorls by immature larvae after fresh needles were consumed. The fate of such larvae is the subject of a later discussion.

Table 2.--Populations surviving the first and second winter

Area	Generations of outbreak numbers	Number of needle miners			
		Spring 1956		Spring 1957	
		Mean	SE	Mean	SE
A	2	14.5	± 1.02	26.10	± 2.35
B	2	17.7	± 1.20	39.60	± 2.32
G	4	31.5	± 2.30	34.62	± 2.60
Dingley Creek	4	32.4	± 1.70	19.08	± 2.40
Cathedral Lake	4	32.2	± 3.00	17.58	± 1.63

Population survival following the second winter, for the 1955 (1953-1955) and 1957 (1955-1957) generations is illustrated by the data in table 3. They show that the population increased in the plots and decreased in the other two areas; the increases ranged from 51 to 515 percent and the decreases 47 to 56 percent respectively of the number maturing in 1955. The decline in the Dingley Creek and Cathedral Lake areas is attributed to depletion of foliage by the larvae before they completed their development. This condition forced them to migrate in search of food or starve.

Table 3.--Number of maturing needle miners after second winter in 1955 and 1957

Plot or area	Generation of outbreak numbers	Number of miners per tip				Percent increase or decrease
		1955		1957		
		Mean	SE	Mean	SE	
A	2	11.63	± 1.18	26.10	± 2.35	+124
B	2	6.43	± 0.71	39.60	± 2.32	+515
C	3	15.12	± 1.64	30.30	± 2.31	+104
G	4	22.97	± 1.46	34.62	± 2.60	+ 51
Dingley Creek	5	35.70	± 2.11	19.08	± 2.40	- 47
Cathedral Lake	4	39.00	± 3.00	17.58	± 1.63	- 56

New infestations

Data on needle miner populations completing development in new outbreak areas in the vicinity of Tuolumne Meadows are shown in table 4. These data are based on counts of larvae and pupae in the terminal (1956) whorl only without regard to those that might have occurred in older foliage. The procedure of sampling only the terminal whorl was used because of the habit of older larvae to migrate forward in late summer and fall to the terminal whorl. As shown in table 4, the results revealed a relatively uniform number of needle miners in each of three areas sampled.

Table 4.--Number of maturing needle miners after second winter in new infestation areas

Area	Generation of outbreak numbers	Number of larvae and pupae per tip Mean		SE	Mortality percent
Soda Springs	1	32.40	±	1.68	25
Lembert Dome	1	26.70	±	2.24	10
Elizabeth Lake trail	1	32.88	±	2.14	8

A comparison of these figures with the data from the same areas, as reported in 1956 (8), revealed a considerable divergence. This discrepancy was attributed to differences in sampling methods which in 1956 included a total count of populations in the latest 5 whorls of foliage. Therefore, the question was immediately raised as to whether depletion of the terminal whorl of foliage by maturing larvae in 1957 had forced many of them to migrate back to the older whorls. To determine this, counts were made from additional tip samples. These counts as shown by table 5 proved conclusively that maturing population data were misleading when taken from only the terminal whorls in new infestation areas.

Table 5.--Average number of pupae in each of the latest 5 needle-whorls (basis 20 tips)

Year of whorl	Number of pupae Mean		SE
1956	10.5	±	1.80
1955	13.1	±	2.24
1954	13.3	±	1.80
1953	15.1	±	2.43
1952	11.8	±	2.26

The populations found were more than twice the number recorded in table 4. The mean population based on all 5 whorls of foliage amounted to 63.8. In another equivalent sample from this area the mean was 78.40. It was thus demonstrated that the sampling of maturing populations in new outbreak areas must always include at least the latest 5 whorls.

The significantly higher total population per tip of 5 whorls in new outbreak areas, compared with that recorded after the first

winter in 1956, is attributed to populations moving forward from further back on the tip where foliage is often retained for 10 or more years. This is illustrated by the example shown below of figures recorded in 1956 from a single tip along Elizabeth Lake trail. [1] Data from 7 other twigs in this area revealed an average of 77 new mines per twig, with variations from 35 to 203 per twig.

Year of whorl	New mines [2]
1946	12
1947	9
1948	4
1949	10
1950	6
1951	7
1952	6
1953	2
1954	2
1955	1
Total (10 years)	59

Factors Affecting Maturity and Emergence

Food supply

A diminishing supply of fresh foliage in older infestation areas became evident in the late autumn 1956. It was most noteworthy in predominantly mature stands, especially in the Dingley and Delaney Creek areas, in the vicinity of Cathedral Lakes, and parts of the Tenaya-Cathedral Creek area. With 3 or more generations of outbreak needle miner populations having preceded this one, the new (1956) foliage grown out was less than half its normal length, besides being greatly reduced in complement.

The poor condition of tree crowns in the fall of 1956, coupled with extremely heavy populations of larvae approaching maturity the next spring, hinted that many larvae would not complete development. In June 1957 vast numbers of larvae in the Dingley and Delaney areas were found spinning down from the tree crowns on silken webs in search of fresh foliage. All understory saplings and even the smallest seedlings were heavily infested and the foliage was mined out. Large numbers of the saplings were completely enveloped in silken tents (figure 2). Each tent contained hundreds of dead larvae. Webbing containing thousands of dead larvae was found around the bases of the large trees.

1/ Not heretofore reported.

2/ One mine per needle, each containing a single larva.

(15729A)

Figure 2.--Young lodgepole pine in heavily defoliated Dingley Creek area enveloped in silken tent. This was formed by needle miner larvae dropping from mined out foliage in the overstory.

In situations where other tree species occurred beneath lodgepole pine, numerous larvae spun down and started mining the foliage of some of these other tree species. Heavy mining, and consequent thinning of the foliage was observed in mountain hemlock, western white pine, white-bark pine, Jeffrey pine, red fir, and white fir. The damage to these trees was minor, resulting possibly in some growth reduction.

The completion of development to adults on these other tree species by maturing needle miner larvae was studied through controlled rearings of infested foliage. These rearings demonstrated the suitability of the other hosts as substitute food in bringing the larvae through to adult moths. Table 6 presents quantitative information from these rearings. The results indicate that red fir, Jeffrey pine, and mountain hemlock were the best substitute hosts.

Table 6.--Number of moths emerging from different host trees from June 24 to August 21

Host tree	Tips in rearing 1/	Moths emerged
Red fir	5	625
Jeffrey pine	3	140
Mountain hemlock	5	104
Western white pine	5	23
White bark pine	6	10
White fir	(3 needles)	1

1/ Each tip comparable in foliage complement.

The dearth of substitute host trees in the vicinity of most lodgepole pines precludes them from being a major factor in sustaining or prolonging an epidemic population. Even if these hosts occurred in abundance they would remain unimportant since needle miner eggs are laid only in lodgepole pine, and the new young larvae feed only in lodgepole pine foliage.

The over-all result of starvation among maturing larvae in older infestation areas is a sharp reduction in populations, as shown by the data for Dingley Creek and Cathedral Lake in table 3. The drop in the Dingley Creek area was 47 percent, and in the Cathedral Lake area 56 percent for the 1957 population as compared to 1955. The downward trend may be expected to continue to near extinction of the populations in these areas by the end of the next generation.

In new infestation areas increasing or sustained high-level populations were found. In the absence of natural control factors, high populations will continue in these areas so long as the foliage supply lasts, during at least the next 2 generations.

Weather

Temperature extremes, the prevalence of prolonged unseasonal temperatures, or temperatures affecting the vital reproductive functions could affect outbreak populations. Such measurements as were made during 1957, however, gave no hint that sub-zero temperatures had adverse effects. The minimum registered at Tuolumne Meadows for the winter of 1956-1957 was -16° F. This temperature extreme did not seem to have a lethal effect on the population. Emergence of moths in this area was the highest recorded during the last two generations. The diurnal and nocturnal temperatures during larval maturity and through pupation were evidently ideal for an early emergence of adults.

Stormy conditions attended by heavy winds and rain during the period from July 6 to 12 caused a heavy drop of mined needles containing pupae. Rearings of 500-needle samples of fallen needles from each of several locations (table 7) showed that all except a very few of the insects died within the needles. The cause of mortality as indicated in 1955 (7) was attributed to high temperatures at the surface of the ground.

Table 7.--Number of living and dead pupae in fallen needles from different areas, July 17-18, 1957

Area	Number of pupae: Living	Number of pupae: Dead
Tenaya Gap	5	149
Tenaya Gap	5	109
Plot G	5	170
Cathedral Creek	1	135
Delaney Creek		
mature trees	10	170
young trees	2	120

Insect enemies

Recognizable parasitism among the earlier instars of the 1955 to 1957 generation was extremely low. As reported previously (8) it amounted to an average of only 0.33 percent of the needle miner population sampled.

The incidence of parasitism in the maturing broods increased in comparison to that in the younger stages. In addition, parasites in 1957 occurred somewhat more frequently among maturing larvae than in 1955 (7). The incidence of parasitism among some 1,182 larvae and pupae from 3 different locations ranged from 5.25 to 20.41 percent (table 8). Parasitism was found to be highest in older infestation areas and lowest in new areas.

Table 8.--Number of parasitized larvae and pupae recognized in 40 tip samples each from 3 areas, July 9-12, 1957

Area	Non-parasitized: Larvae	Non-parasitized: Pupae	Parasitized larvae and pupae	Percent parasitized
Soda Springs	3	376	21	5.25
Tenaya Gap	7	361	22	5.64
Dingley Creek	6	306	80	20.41

Parasites reared from needle miner-infested tips provided information on species composition. These were taken between August 3 and 21 from 4 emergence cages, each containing 100 tips from different areas. The species have not been determined fully, but specimens have been preserved and will be sorted and identified. The separations that have been made are shown in table 9. They revealed that on a numerical basis the encyrtid Copidosoma sp. outnumbered by nearly 3 times all other species combined.

Table 9.--Parasite incidence by recognizable species reared from 100 tips each from 4 areas

Area	Number of parasites emerged			
	Copidosoma	Apanteles	Other	Total
Soda Springs	1,000	11	50	1,061
Cathedral Creek (new) 1/	467	16	228	711
Cathedral Creek (old) 2/	347	6	353	706
Delaney	282	6	60	348

1/ New infestation--one generation only.
2/ Old infestation--2 or more generations.

The numerical superiority of Copidosoma sp. over the other species is due in part to its polyembryonic character, which results in 10 to 12 adults emerging from a single needle miner larva, and in part to evident synchronization of its life cycle with that of the host. The maximum emergence of this parasite occurred just subsequent to heaviest oviposition by the needle miner.

The close association between Copidosoma and the needle miner was demonstrated by observations of mating and oviposition. Approximately 50 parasitic adults were placed in a petri dish containing 100 needle miner eggs. The observations under 40-power magnification as recorded are quoted below.

> "Intense excitement was registered by rapid movement to, fro, and around a group of needle miner eggs. Probing by antennae was thorough before attempts to oviposit. This consisted of 'feeling' all parts of an egg and egg group. Subsequent to each 'feeling' a female would back up to an egg or hover over it, then after unsheathing the ovipositor, attempt to insert it into an egg. Under 40-power magnification the barely visible ovipositor was seen to bend on contact with

the egg integument, then straighten as it entered the egg. Once the ovipositor was within the egg the parasite adult remained quiescent for approximately 15 or more seconds before withdrawal."

Birds

Observations by W.L. Muhlbach revealed that several species of birds contribute in some measure to the natural control of the needle miner. Some were observed feeding on larvae, others on adult moths in flight. Still others were suspected but were not actually seen to feed on both stages. Those identified through use of Peterson's key (4) are listed below.

1. Observed feeding on larvae.
   Mountain chickadee, *Penthestes atricapillus*
   (Western) warbling vireo, *Vireo gilvus swainsoni*
   Audubon's warbler, *Dendroica auduboni*
   Cassin's purple finch, *Carpodacus cassini*
   Oregon junco, *Junco oreganus*

2. Suspected to feed on larvae.
   Western tanager, *Piranga ludoviciana*
   Pine siskin, *Spinus pinus pinus*

3. Observed feeding on moths.
   Western wood pewee, *Myiochanes richardsoni richardsoni*
   Hammond's flycatcher, *Empidonax hammondi*
   Audubon's warbler, *Dendroica auduboni*
   Calaveras warbler, *Vermivora ruficapilla ridgwayi*

Pupation Habits

A unique prepupal stage in the life cycle of the needle miner was reported by F.D. Morgan early in 1955. Morgan described this stage in detail (2) and included in his report photographic illustrations of it. However, it was suspected that this may have been an abnormality. The occurrence of this stage in a normal life cycle of the needle miner was the subject of additional detailed checking under laboratory and field conditions during 1957.

In the laboratory 4th instar larvae were planted on fresh lodgepole pine tips kept fresh by inserting the stems in water. A total of 200 larvae were established in this manner. Weekly examinations were made to record development, survival, mortality and the causes thereof. These rearings were continued from March 14 to April 12, 1957.

The results revealed that: (1) among 28 specimens reaching the pupal stage none exhibited a special prepupal form; (2) twenty-six of

the 28 pupae emerged as normal adults, while 2 died; (3) forty-two of the larvae died, of which 12 percent were parasitized; (4) the balance of larvae planted initially were lost.

This information was supplemented in the field during June 1957 when examinations were made of over 1,800 maturing larvae and pupae. These examinations revealed no unique prepupal stage of the type described by Morgan. Some variations of pupal color phases were observed, but these variations were transitory and lasted for a period of 24 hours or less before the pupae reached their normal jet-black coloration. Newly formed orange, pink, and lemon-yellow pupae were observed. These colors probably stemmed from the colors of the last stage larval forms.

It was concluded as a result of the laboratory rearings and field observations that normally there is no unique black prepupal stage. However, the occurrence of such a stage was found to develop as a malformation from last stage larvae when the latter were removed from the needles and held in a petri dish. Some of the larvae reared in this manner were not able to pupate normally, and monstrosities resulted which did not complete development to the adult stage, due probably to the abnormal environment.

The incidence of pupation in the field during 1957 was based on samples taken from 8 different localities of the needle miner outbreak area. The earliest instance was recorded June 8 in the vicinity of Soda Springs in Tuolumne Meadows. Two weeks later records from all areas representing both old and new infestations revealed an average incidence in excess of 80 percent pupation. Thus, within a 2-week period it was evident that a rapid transformation had taken place from last stage larva to pupa, indicating the maturity of the 1955-1957 generation.

ESTABLISHING THE NEW (1957-1959) GENERATION

Period, number, and sex of emerging moths

Information on the emergence period, and on the number and sex distribution of moths in 1957 was obtained largely from observations on infested material held in rearing at Tuolumne Meadows. Four cages, each containing 100 tips, were established on July 3 and 4, 1957. The tips were collected from Delaney Creek, Cathedral Creek (old infestations), Soda Springs, and Cathedral Creek (new infestations). Tips from the new infestation areas included the latest 5 whorls. Those from the older infestations contained primarily the 1956 foliage whorl, the older previously mined foliage having dropped away.

The first emergence occurred on July 7 from the Soda Springs material. From that date forward emergence took place at an increasing tempo, with a peak occurring between July 25 and 30 for all caged

material. Emergence was completed August 5 for Soda Springs, and ended August 10 for all other caged material. Emergence curves for the 4 areas is shown by figure 3.

The total emergence by sexes for each of these cages is shown in table 10. A very high population of moths came from this material which can be considered fully representative of the areas of origin. The populations in the two new areas of infestation represent the total from 5 whorls, while that from the older areas represents the total from only the terminal whorl. This emergence is possibly 10 percent of the initially established population, shedding some light on the enormity of populations produced in this outbreak.

Table 10.--Number of needle miner moths emerged

Area	Number of moths			
	Males	Females	Total	Per tip
Soda Springs	2,055	1,541	3,596	36.0
Cathedral Creek (new infestation)	1,447	1,431	2,878	29.0
Delaney	1,037	950	1,987	20.0
Cathedral Creek (old infestation)	786	926	1,712	17.0
Total	5,325	4,848	10,173	

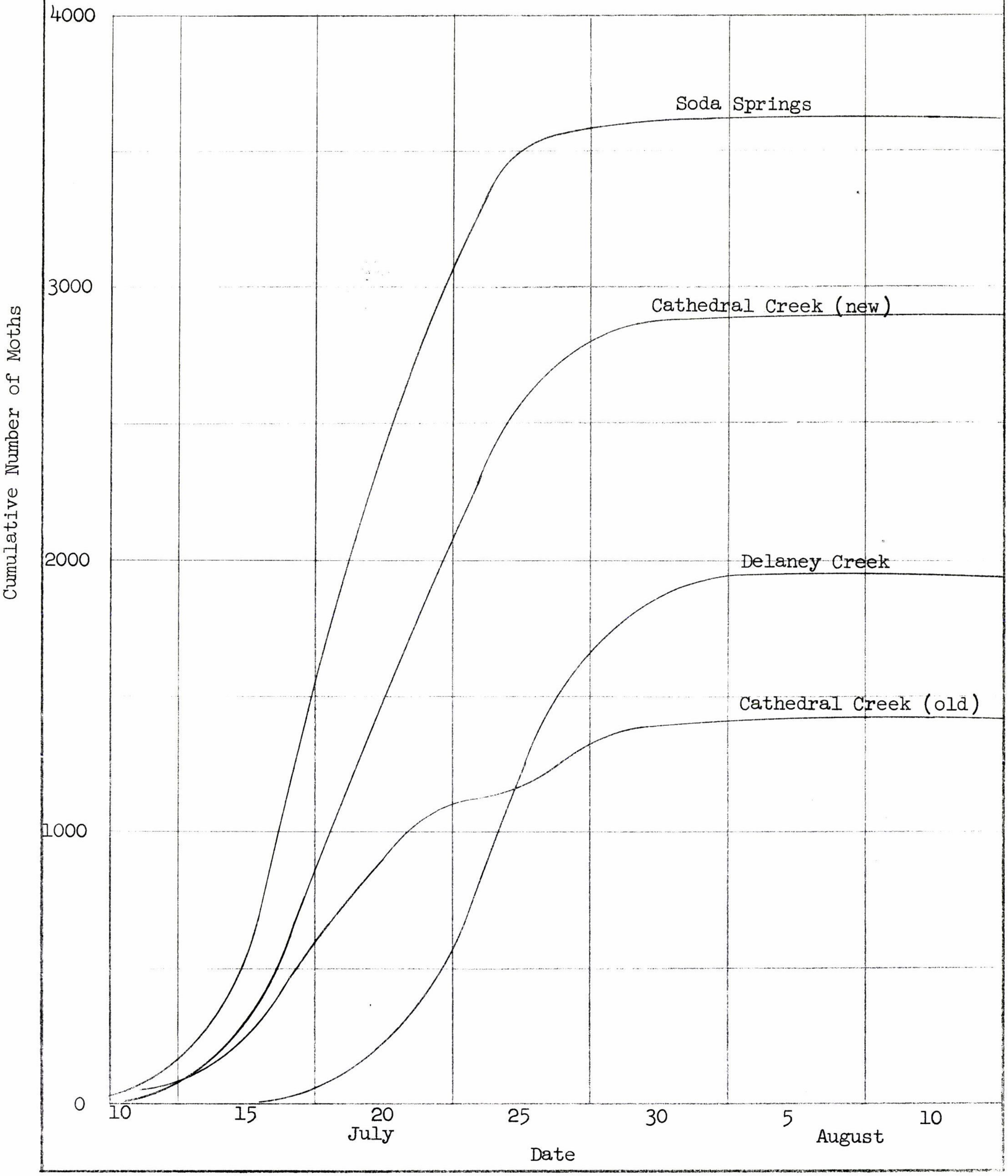
The distribution of sexes was nearly equal. The proportion was 1 male to 0.91 female.

Records for the 30-day period during which emergence took place revealed that: (1) during the first 10 days 74 percent of adults emerging were males; (2) during the next 10 days 57 percent of emerging adults were females; and (3) during the last 10 days 81 percent of the adults emerging were females. More than 83 percent of the total emergence took place during the first 20 days.

These facts indicate that eggs would not be deposited in numbers during the first 10 days of the flight period. Previously the scarcity of eggs until about the 3rd week of flight was attributed to sexual immaturity of females. While this may be true in some instances, examinations of newly emerged females revealed fully formed eggs.

Information was obtained on the emergence of males and females at different times of day during the emergence period. The collections were timed for 10:00 a.m.; 2:00 p.m.; 4:00 p.m.; and 6:00 p.m.

Figure 3.--Lodgepole needle miner emergence in 1957 from four areas - (Basis: 100 tips/25 trees each area)



The data are summarized in table 11. They show that females tended to emerge earlier in the day than males, with twice as many as males by 10:00 a.m. Between 10:00 a.m. and 4:00 p.m. the proportion of males to females was nearly equal, with a slight superiority in number of males. Between 4:00 p.m. and 6:00 p.m. males outnumbered females by 2.7 to 1. These facts tend to show a provision by nature to assure an abundance of males in the evening hours when mating takes place.

Table 11.--Number of males and females emerging at different times during the day

Time (PDT)	Number of moths emerging		
	Males	Females	Percent males
10:00 a.m.	754	1,484	33.6
2:00 p.m.	1,536	1,411	52.1
4:00 p.m.	1,463	1,388	51.3
6:00 p.m.	1,394	522	72.7

Flight observations

Observations during flight in 1955 (7) revealed mass movements of moths under the influence of light wind movement. Additional more detailed observations in 1957 confirmed the earlier records and also gave conclusive evidence of the role of local air movement in the dispersal and spread of infestations.

The 1957 observations were begun July 15, about a week after the first moths appeared in emergence cages. They were continued intermittently until the flight period ended. While most of the observations were taken in the Tenaya Gap area, others were made in Tuolumne Meadows near the west face of Lembert Dome, at the base camp, at the 8,000 and 9,200 foot elevation temperature recording stations, on top of Lembert Dome, along the Gaylor Lakes trail, at the base of Mammoth Peak, Lyle Fork basin, and Rafferty Creek basin.

These observations were made primarily for information on relative number, flight direction, and drift of moths into new areas. Air movement, light intensity, and temperature were each recognized as strong stimuli bearing on flight behavior. Measurements of these factors along with flight observations were taken insofar as possible.

The flight observations in the Tenaya Gap area on July 15 revealed that emergence of moths under field conditions was well under way. At that time most of them were inclined to adhere closely to

the crowns of trees because of strong air movement. Moth flight was more evident in dense clusters of trees which served to break the force of the wind.

Weekly observations just prior to sundown (6:45 to 8:30 p.m. PDT) were continued through August 2. They revealed a gradual pickup in the number of moths drifting northward on light air currents, from dozens per minute at first to countless thousands per minute on the later date. This confirmed previous observations that the adult moth is influenced in its flight direction by light air movement.

Great differences in the number of moths in flight, from none to many thousands per minute, were noted in the course of a single evening. At 7:15 p.m. when air movement from the south was estimated between 1 and 3 m.p.h., moth migration was barely discernible. At 7:30 p.m. an increase in air movement to an estimated 6 to 8 m.p.h. resulted in a pronounced drift of moths northward. At 7:45 p.m. a drop of air movement again to 1 to 3 m.p.h. resulted in only a slight tendency to drift. At 8:00 p.m. the air was completely calm and moth flight was aimless, with no tendency to drift.

Observations on the flight habits of moths in other areas confirmed these notations on moth behavior with respect to air movement. At Tuolumne Meadows, directly west of Lembert Dome, a record taken just before sunset, August 2, revealed the air was filled with moths, all drifting southward on a very light north-south breeze. Along the southeast slopes of Lembert Dome on August 3, evening flights were southeastward on light winds. On the crest of Lembert Dome the moth flight was generally eastward, and sustained by light air movement in the evening.

Influence of temperature

Recording hygrothermographs 3/ were established in standard instrument shelters at 3 elevations: (1)9,200 feet, the upper limits of new outbreak populations east of Tuolumne Meadows; (2) 8,600 feet, base camp location and representative of eastward extensions of outbreak populations; (3) 8,000 feet, south of Tenaya Lake and representative of lower elevation limits of outbreak populations.

Physiographic differences between these stations were recognized. The upper station was located on the crest of a ridge; the intermediate station was near the bottom of a south-facing slope; and the lower station in the bottom of a basin. All stations were situated similarly with respect to lodgepole pine cover.

3/ Only the temperature recordings were used in this study. The humidity records were too unreliable for use in comparison with psychrometer measurements.

Failure of the clock mechanism in the instrument at the 9,200-foot elevation prevented the record from being complete. However, sufficient information was obtained to show that differences were so slight in comparison with the 8,600-foot record that the measurements at the higher elevation were a duplication. Slightly higher minimum temperatures were recorded at the upper level, evidently due to air drainage.

Daily maximum and minimum temperatures at the intermediate (base camp) and the lower (Tenaya Lake) stations are plotted in figure 4 for the period July 1 to August 19. Most of the needle miner emergence, mating, and egg-laying period takes place during this period.

As shown by the chart the temperature differences at these locations were so slight as to have little or no influence on needle miner behavior. A somewhat broader spread, with higher maximum and lower minimums than the Tenaya Lake station occurred at the base camp station. Divergence at the maximum end amounted to only 5 degrees for a single day, while most days rose the same or differed from 1 to 3 degrees. At the minimum end the same trend was shown; the greatest divergence for a single day was 13 degrees.

The pattern of daily temperature fluctuations during the period from July 1 to August 19 was similar at each location. The minimum temperature occurred between 6:30 and 7:30 a.m. (PST); thereafter, the temperature rose rapidly to reach a maximum between 12:00 noon and 2:00 p.m. (PST). After 2:00 p.m. (PST) it declined slowly. These close similarities in temperature pattern indicated little likelihood of any influence on needle miner behavior.

Distinct differences in needle miner abundance were observed at all locations during flight. At the base camp location, moths occurred in abundance, with the greatest amount of free flight between 3:00 and 5:30 p.m. (PST), and the greatest activity in tree crowns from 5:30 to 8:00 p.m. (PST). In contrast, at the Tenaya Lake station, moths observed in free flight were barely discernible; only 3 were seen passing a given point during 15 minutes on August 8, just past the flight peak. The dearth of moths here was due to the absence of infestations to the south. Observations on moth flight at the 9,200-foot station also revealed lower populations as compared with the base camp station. The number of moths drifting and in the tree crowns at the 9,200-foot level was considerably less. At the same time the number was greater than at the Tenaya station. A possible reason for the fewer numbers here is the influence of greater air movement on the ridge top.

Comparative egg counts from ten 5-whorl tips at each location on August 8 revealed 66 eggs at the base camp station, 6 eggs at the Tenaya station, and 10 eggs at the highest station.

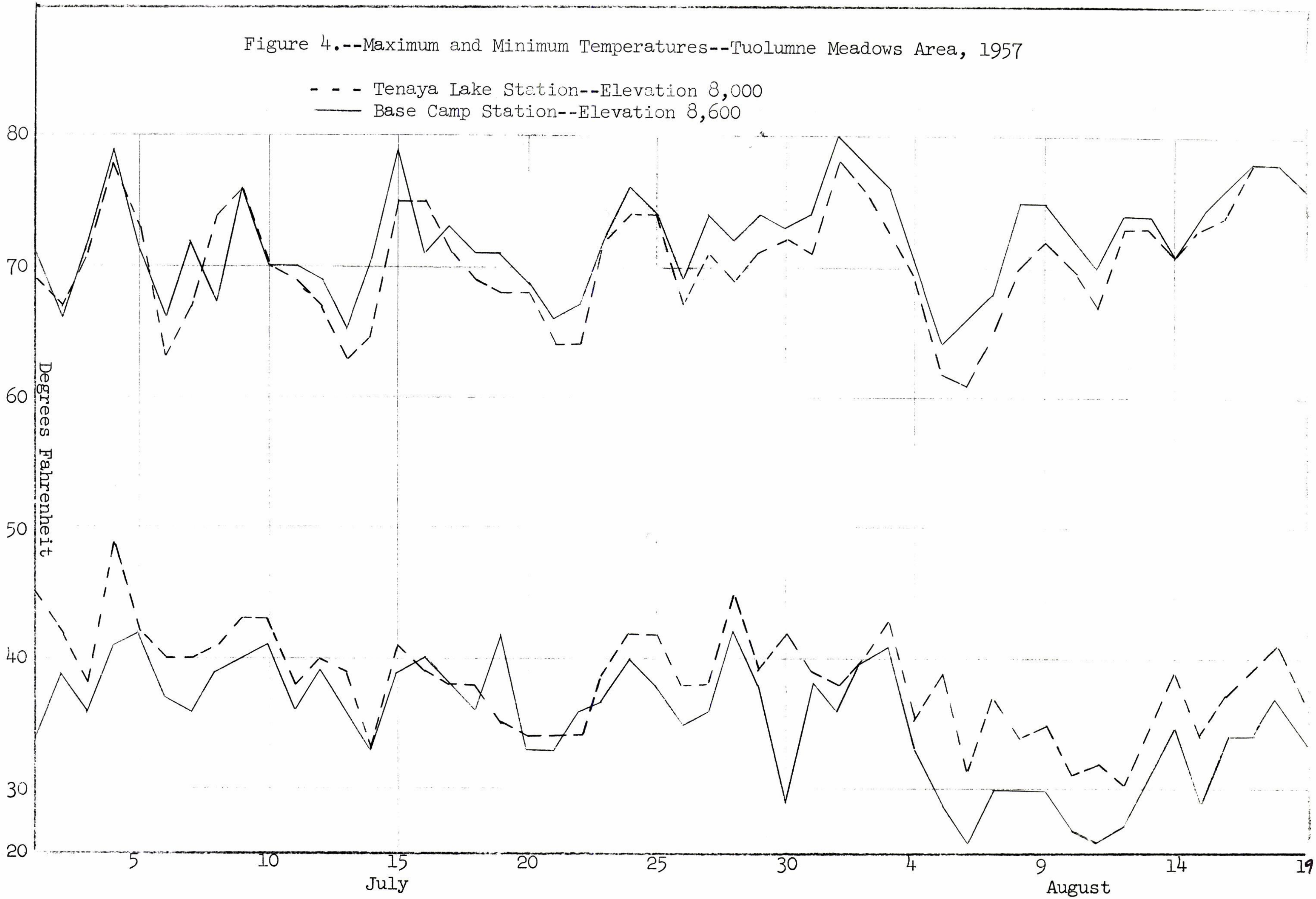


Figure 4.--Maximum and Minimum Temperatures--Tuolumne Meadows Area, 1957
- - - Tenaya Lake Station--Elevation 8,000
—— Base Camp Station--Elevation 8,600
Degrees Fahrenheit
80
70
60
50
40
30
20
5
10
15
20
25
30
4
9
14
19
July
August

Courtship and mating

Because of a great preponderance of males over females early in the emergence period, few mating pairs were observed until the last few days in July. From then on for a period of 10 days mating pairs were common in the evening hours. Courtship and mating habits of the moths were observed between 7:00 and 8:30 p.m. (PDT). Considerable wing fluttering, rapid antennal movement, and running by paired adults prior to copulation was observed. This activity, interpreted as a courting gesture, invariably preceded copulation. Copulating pairs were most numerous after 7:30 p.m. (PDT). Temperatures recorded during observations on mating behavior varied from 52 to 60° F.

Diminishing light intensity was thought in 1955 to have some influence on flight and mating habits. Attempts were made in 1957 to measure this factor and relate the results to moth behavior in these respects. This was done by use of a Weston light meter during a single evening. The results of observations made on August 2, 1957 are summarized below. The light factor is included along with temperature and wind velocity.

Time (PDT)	Temp.° F.	Light factor Weston units	Wind vel. m.p.h. estim.	Observation on moth activity
7:00-7:15 p.m.	65	36	1-3 (N)	Flight-thousands-light drift N
7:30 p.m.	64	30	6-8 (N)	Flight-thousands-strong drift N
8:00 p.m.	58	27	0	Courtship gestures, thousands in air - no drift
8:15 p.m.		24	6-8 (S)	Thousands flight-drift southward
8:25 p.m.	52	9	0	Flight greatly reduced; moths crawling among lodgepole tips; increase in mating pairs.
8:30 p.m.		7	0	3 mating pairs observed

These observations do not suggest any special differences in the influence of temperature as compared to light on moth behavior. All that may be said at present is that moth behavior was the result of responses to both factors. Controlled experimentation may reveal differences. The response to air movement was more clearly marked.

Longevity of moths

The life span of adult moths is short, lasting probably not over 3 weeks. Thousands of dead moths on still water surfaces were commonly observed within 2 weeks after the peak of emergence (figure 5). Some conception of moth longevity was learned by collecting adults daily from the surface of water in wash tubs. The collections were made at the Tuolumne Meadows base camp each 24 hours for 18 days, beginning August 2. The counts are summarized in table 13. They show that the highest number of moths was collected during the first 5 days. The collections during this period were more than twice the number taken during the next 8 days. It seems evident from these limited data that the incidence of moth mortality was high within 3 to 4 weeks after the beginning of emergence. The proportion of dead males and females collected in this experiment indicates that high mortality of males may have taken place before the collections were started.

(15906)

Figure 5.--Accumulation of thousands of dead moths in still pond in Tuolumne Meadows 2 weeks after peak emergence had occurred.

Table 12.--Number and sex of dead moths taken from water surface in tubs at base camp

Date 1957	Number of dead moths		
	Males	Females	Total
August 2-7	117	171	288
8-12	23	109	132
13-20	23	83	106
Total	163	363	526

Spread of new infestations

Observations were made during the latter part of the flight period to observe the number of moths in lodgepole pine forests previously uninfested. The observations were concentrated in stands lying to the northeast, east, and immediately adjacent to existing heavy infestations. These stands were in the direct path of prevailing air currents and most vulnerable to attacks by moths drifting into them. The observations were at locations along the trail toward Gaylor Lakes, at the base of Mammoth Peak, in stands along Lyle Fork and in the Rafferty Creek drainage basin.

Moths were found in all areas, from 2 to 4 miles eastward from the previous extension of outbreak infestations. They were numerous generally within 2 miles of the outbreak, and relatively few in number at 4 miles, indicating the possibility of a 2-mile eastward extension of the outbreak. This is roughly in an arc extending from the south of Lower Gaylor Lake to the lower part of Lyle Fork and Rafferty Creek basins. The possibility exists that light infestations may develop in all stands within 1 to 2 miles east of this arc.

Egg incidence and location

Oviposition was not observed, but as reported in 1955 this act was found to take place from twilight to late in the evening. The first eggs were found in the field on July 23, when 2 of them were recorded from 10 tips examined. The incidence of eggs for the 1957-1959 generation is shown in table 13. Listed in this table are the number of eggs found each week in 10 tips taken from 4 areas sampled for a period of 4 weeks.

The data show that the egg laying began during the 4th week in July and reached a peak 2 weeks later. The 2-week lag between emergence of the first moths (July 7) and deposition of the first eggs (July 24-26) is probably due to the lag in emergence of females. Males were predominant during the first 2 weeks, with females catching up afterward.

Table 13.--Number of eggs each week from 10 tips in 4 areas sampled

Area	Number of eggs recorded--1957				
	7/24-26	7/31-8/1	8/6-7	8/12-13	8/19-21
Delaney	0	19	24	48	49
Plot G	0	17	102	46	92
Soda Springs	4	13	90	53	53
Lembert Dome	10	12	19	19	19

Additional information, heretofore unreported, on the location of eggs was obtained in 1957. In areas previously uninfested, eggs were found under bark scales along the stem, for a distance of 14 inches back of the twig terminal. A few were found in the scales at the bases of the needle sheaths of old needles. A large group of eggs was uncovered from the edge of an old healing scar. Eggs are often laid in old mined needles (figure 6).

Incubation and hatching of eggs

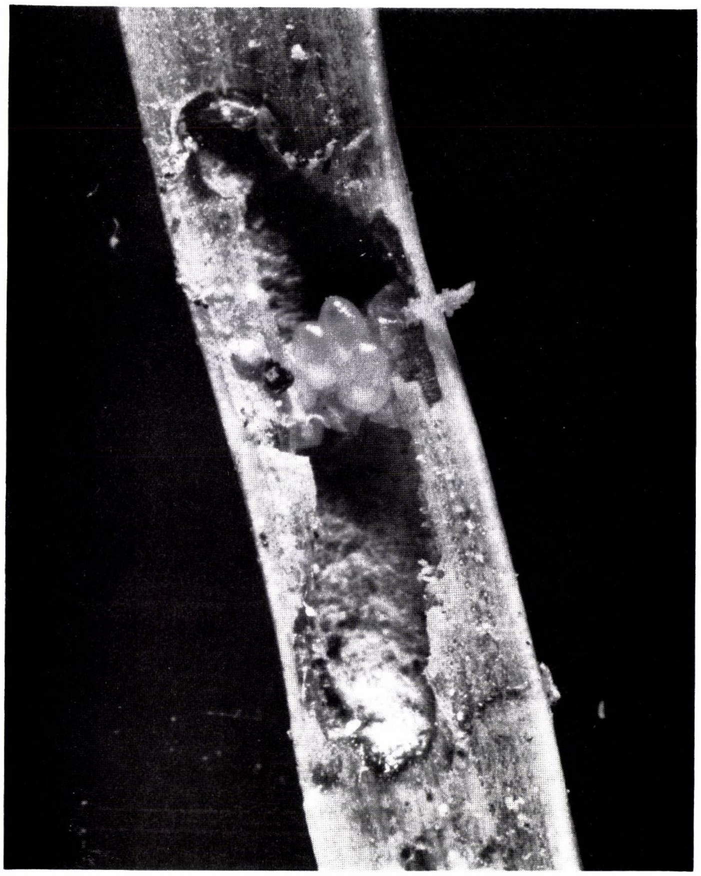
Information on the incubation and hatching of needle miner eggs in 1957 was obtained from collections of eggs held in petri dishes, and from periodic samplings of tips taken from different areas. A total of 200 eggs collected July 31 to August 21 were held in petri dishes on blotting paper. Moisture was supplied by adding droplets of water to the blotting paper every 2 days. The first egg hatched on August 21. By September 5, 44, or 22 percent, of the original number had hatched. Of the remaining 156 eggs, 129 were in the black-headed stage ready to hatch and 27 were dried out on the later date.

Tip collections taken to follow the progress of egg development were made each week beginning August 28 and ending September 11. Each tip collection consisted of 10 tips each from 4 representative locations: one in Tuolumne Meadows, two areas in Cathedral Creek basin, and one in Delaney Creek. The data from these tips included some 620 eggs, and in addition on September 11 some 83 empty chorions, and 183 entries into foliage by newly hatched larvae. These data revealed that 45 percent of the eggs were ready to hatch on August 29, 91 percent ready on September 5, and over 94 percent on September 11. On the latter date the ratio of eggs to new entries was 1:1.05. At that time empty chorions from newly hatched eggs were found commonly.

These data indicated that the hatching of all eggs and the entry into foliage by first-stage larvae would be completed by the 3rd or 4th week in September.

Populations of newly established larvae

Populations of needle miner larvae established in the 1957-1959 generation were determined from tip samples taken in mid-October. These samples were from areas representing: (1) no previous outbreak infestations; (2) one generation of outbreak infestations; and (3) two or more generations of outbreak infestations. A 100 percent check was made of all infested needles in the latest 5 whorls of 40 tips each from areas having no previous outbreak infestations. Sufficient tip samples were taken to fall within or close to a 10 percent sampling error in areas having one or more outbreak generations. From 40 to 100 tips were required in one generation outbreak areas, and 40 tips in 2 or more generation outbreak areas.



(15899)

Figure 6.--Group of needle miner eggs in old mined needle. This is a favored location. X20

Actual samplings from tips collected were of populations in the terminal whorl of needles for all tips except those taken in areas not previously infested. In the new areas a 100 percent examination was made of all needles in the latest 5 whorls. A summary of data by areas is given by table 14.

Table 14.--Number of established first-stage larvae in needles, October 1957

Age of infestation	Area	Number of larvae/tip Mean	SE	Basis
No previous outbreak	Mammoth	0.30	± 0.00	Total population last 5 whorls
	Gaylor Lakes trail	2.72	± 0.00	
	Dana Fork 9,200 ft.	2.60	± 0.00	
One outbreak generation	Base Camp	15.30	± 2.48	10-needle sample of latest whorl
	Elizabeth Lake trail	13.08	± 2.47	
	Soda Springs	33.78	± 3.10	
Two or more outbreak generations	Delaney Creek	21.00	± 1.73	10-needle sample of latest whorl
	East Cathedral	21.70	± 2.09	
	Cathedral Lakes	12.66	± 2.12	
	Plot G	47.40	± 2.49	

The number of larvae established in 1955 and 1957 for 5 of the areas listed in the previous table are shown in table 15. These data provide some basis for indicating some points in regard to the future course of the outbreak in certain locations.

Table 15.--First stage larval populations established in 1955 and 1957

Age of infestation	Area	Number of larvae per tip 1/					
		1955			1957		
		Mean		SE	Mean		SE
One outbreak generation	Soda Springs	14.82	±	3.06	33.78	±	3.10
Two or more outbreak generations	Plot G	24.78	±	1.76	47.40	±	2.49
	Delaney Creek	52.50	±	2/ 2.40	21.00	±	1.73
	Cathedral Lakes	38.30	±	2/ 3.90	12.66	±	2.12
	East Cathedral	48.70	±	2/ 3.10	21.70	±	2.09

1/ Latest whorl only.

2/ Basis: July 1956 counts after first winter.

There seems to be considerable evidence to indicate a population decline over the previous generation, especially in older areas of infestation. The points which seem worth consideration are:

1. Populations of newly established larvae in areas previously uninfested by outbreak populations were less than anticipated. However, the data may be too limited to be conclusive.

2. Populations of newly established larvae were larger than in 1955 in the area infested previously by one generation, but the increase proportionally was not as great as the increase in 1955 over 1953.

3. The population increase in Plot G was at variance with all other older age infestation areas, where sharp declines occurred. Two reasons why this happened are: (1) the stands of Plot G are generally younger and suffered less from previous defoliations, as indicated by longer needles and fuller complement of terminal foliage; (2) the location was strategic from the standpoint of drift of countless numbers of moths from the south.

4. Sharp declines in populations established in 1957 compared with 1955 occurred in all other older infestation areas. The reason is attributed primarily to the great reduction in needles in these areas.

EFFECT OF DEFOLIATION ON GROWTH INCREMENT OF LODGEPOLE PINE

The fact that needle miner defoliations depress the growth rate of lodgepole pine is well known, but the effect of defoliation on growth has not been studied in detail in any of the Yosemite outbreaks. Shortened foliage, fewer needles, and shortened internodes are among the more immediate noticeable effects of defoliation (figure 7). Depressed radial increment is nonetheless immediate in effect, but is not seen without boring and removing increment cores or by obtaining cross sections of stems.

(15904)

Figure 7.--Lodgepole pine with normal foliage (left), in contrast to one that has been defoliated by a single generation of needle miners (right).

Preliminary studies on growth reduction were begun in 1957. These were done through measurements of annual radial increment covering a span of years sufficient to include one or more periods of needle miner outbreak. The period from 1890 to the present was judged to be long enough to cover at least one outbreak previous to the current one.

Two areas were selected for this study: (1) the Delaney Creek basin, having a predominantly southwest-facing slope; and (2) a location northeast of Cathedral Peak characterized by meadows, ridge crest, and generally north-facing slopes. These areas differed somewhat as to past infestation history, in other tree species associated with lodgepole pine, and in physiographic features.

The trees selected were in 3 categories for each area: (1) mature lodgepole pine having survived at least one major outbreak period preceding the current outbreak; (2) young lodgepole pine having grown up from poles since the last major outbreak; (3) other tree species approaching or having reached maturity as checks. The check trees used at the Delaney Creek location were all mature red fir. Those at the Cathedral Peak location were divided equally between maturing western white pine and mountain hemlock. A total of 30 trees was included in each category. All trees in each group were numbered serially.

Increment cores were taken from the main stem of each tree at 4 feet above the ground by means of a Swedish increment borer. Those taken from mature lodgepole pine and other tree species were bored deep enough to include at least the 1890 annual ring. Those taken from young lodgepole pines were bored deep enough to include the 1930 ring. All cores were numbered and labelled as to area, age, and tree species. They were measured under a binocular microscope with an increment core measuring machine. Ring widths were recorded in thousandths of an inch.

The growth curves plotted from summarized data for each location are shown in figures 8,9, and 10. These curves are all based on the mean annual and periodic annual growth rate of 30 trees included in each group. Measurements for both the mature lodgepole and check trees date from 1890. Measurements for the young lodgepole pines date from 1930.

The data from both areas show an almost identical growth pattern in the mature lodgepole pine (figures 8 and 9). This is characterized by a gradual decline, followed by an abrupt drop, then a period of recovery. This is in turn followed by a repetition of these events. The sudden drop in growth rate in each case is coincident with recorded needle miner outbreaks, leaving no doubt of their effect. The same pattern was exhibited by young trees from records dating from 1930, with a more abrupt growth decline after 1950 than shown by the mature trees (figure 10).

When compared with other tree species growing in the same areas, the depressed growth rate resulting from needle miner defoliations is

Figure 8.--Mean Annual and Periodic Annual Growth Rate for Mature Lodgepole Pine and Red Fir, Delaney Creek Area

- - - 30 Lodgepole pine
——— 30 Check trees (Red fir)

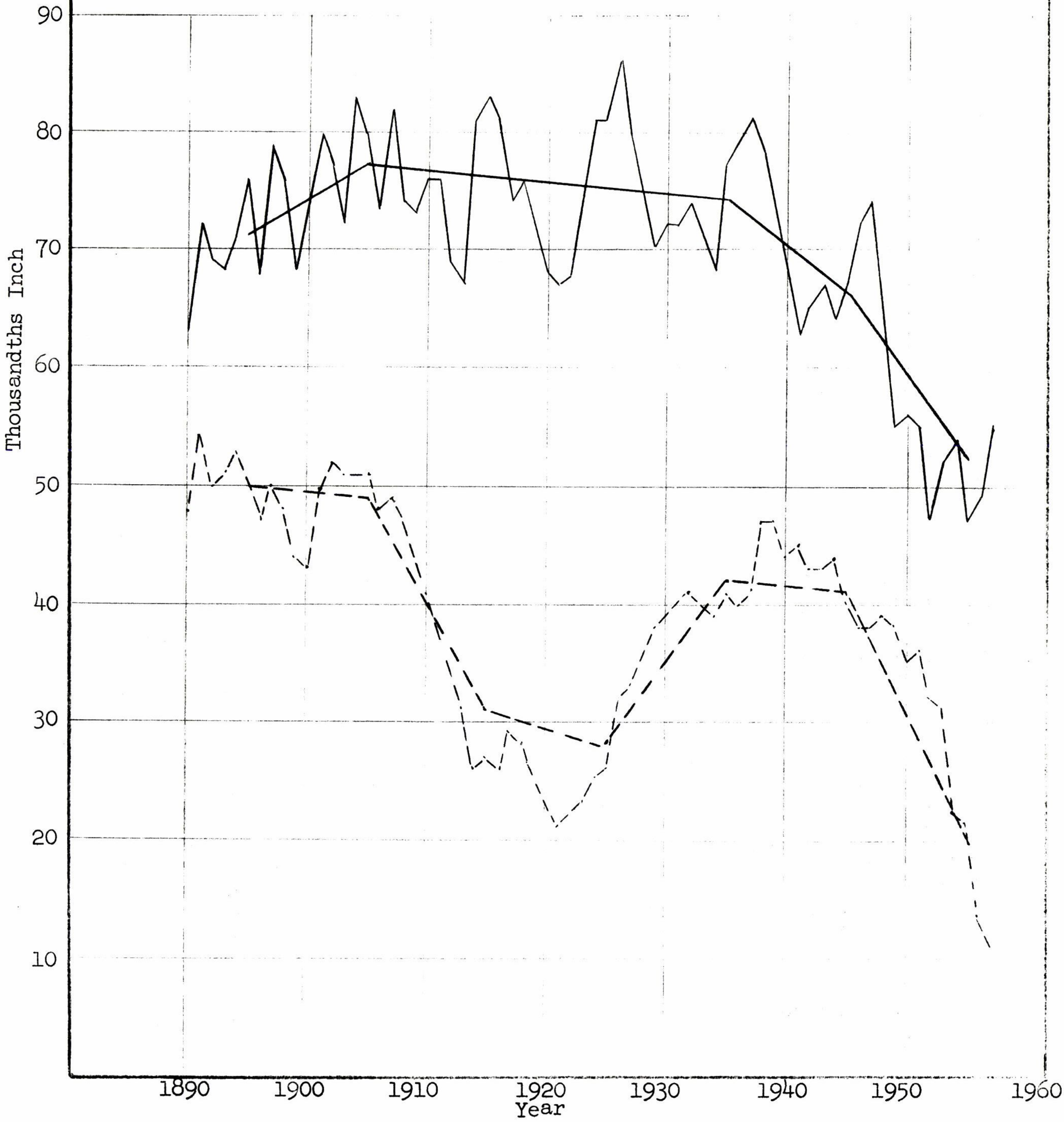


Figure 9.--Mean Annual and Periodic Annual Growth Rate for Mature Lodgepole Pine and Other Tree Species, East Cathedral Area

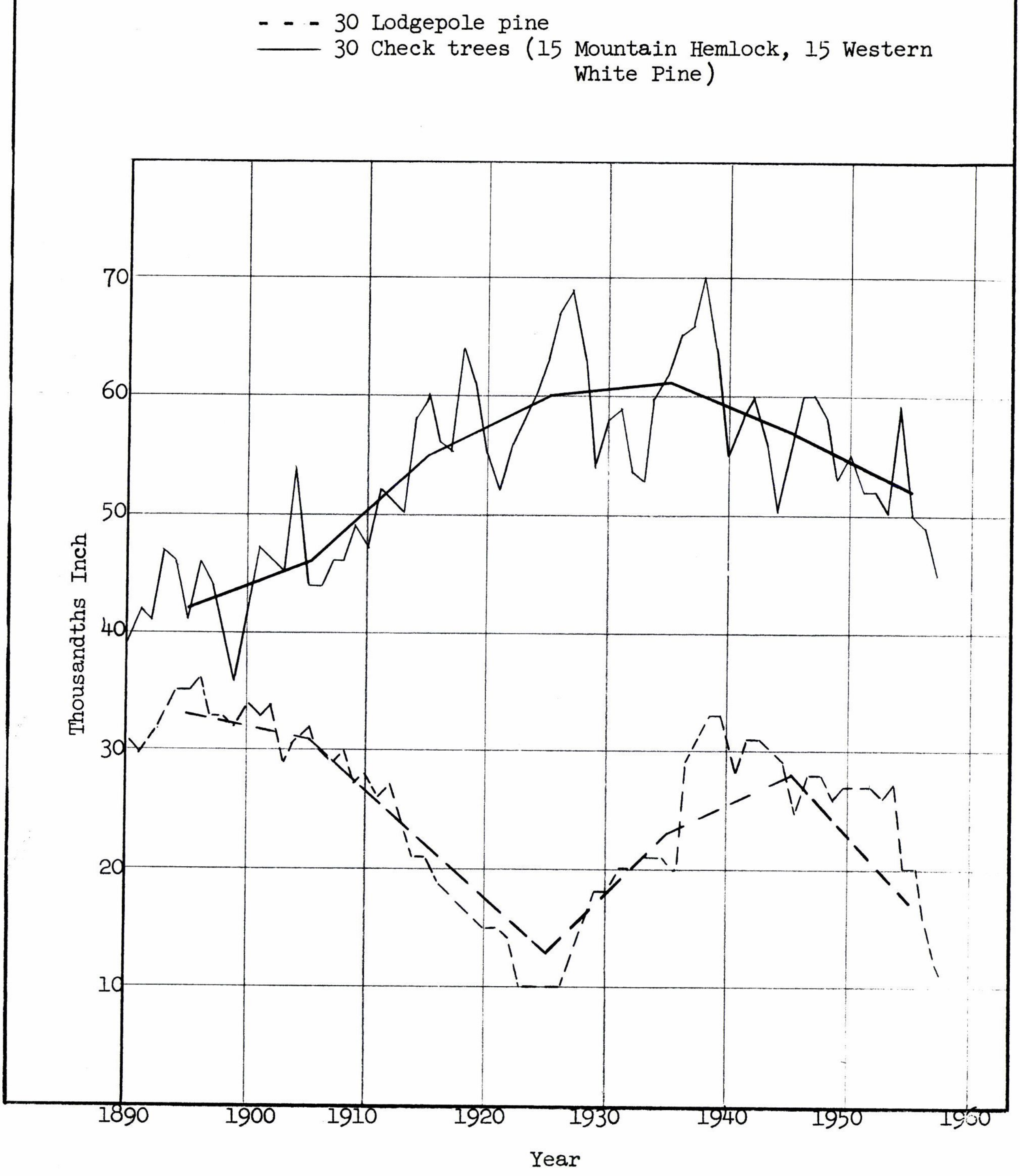
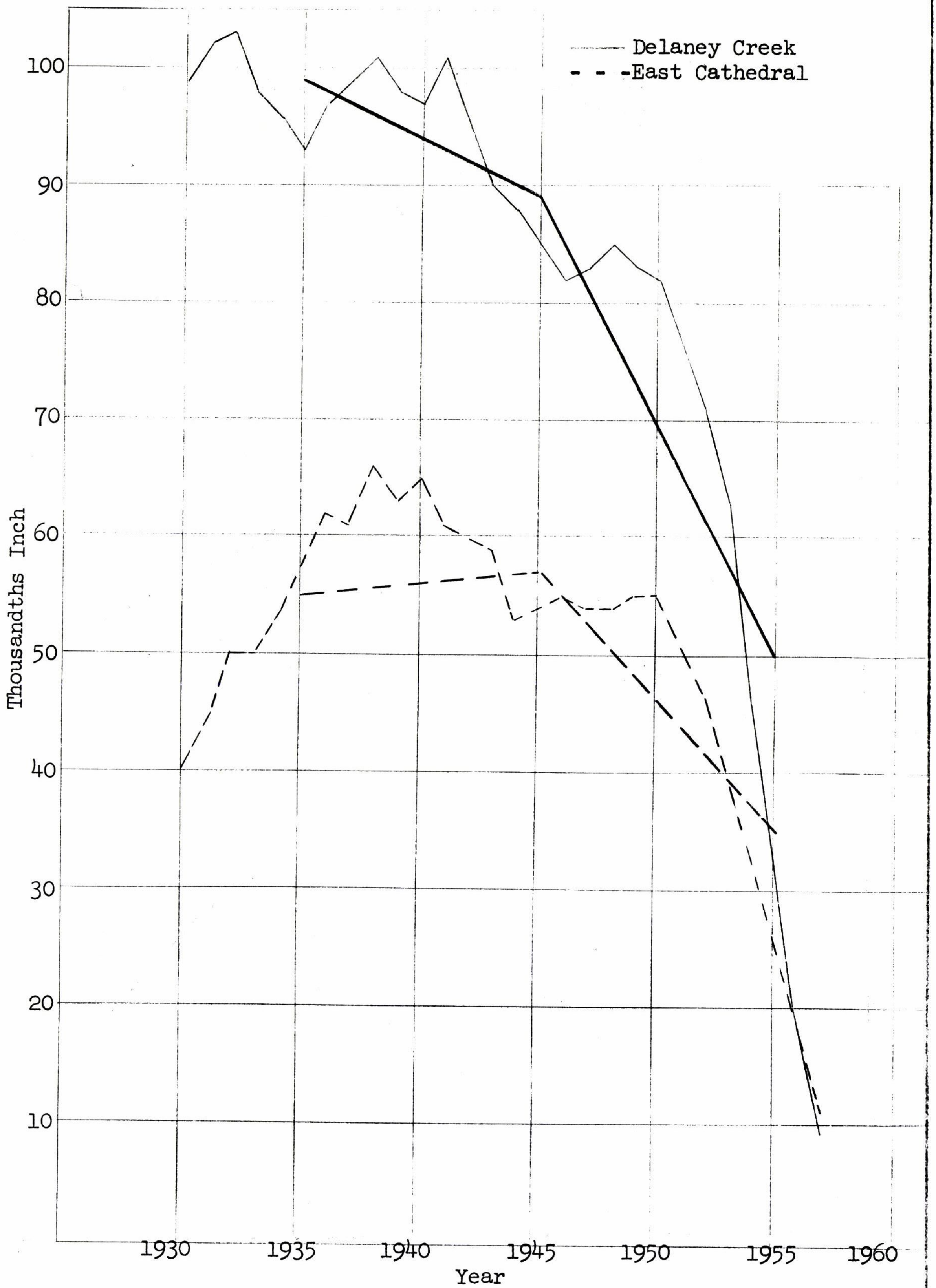


Figure 10.--Mean Annual and Periodic Annual Growth Rate for 30 Young Lodgepole Pines Each in Delaney Creek and East Cathedral Areas



more striking. Check trees in the Delaney area (figure 8) revealed only a slight decline in growth rate during the period from 1905 through 1935, when lodgepole pines suffered a long period of decline and recovery from a recorded outbreak lasting from 1910 to 1922. During this period the check trees in the east Cathedral area (figure 9) gradually increased in growth rate, with differences in comparison to the Delaney checks attributable to site, slope, tree species, and elevation. Decreasing growth rates were characteristic among the check trees in both areas since 1935, indicating the possibility of inhibiting climatic effects or a decline owing to stand maturity. The same decline showing in young lodgepole pines, however, tends to discredit the possibility that stand maturity was a factor.

The sudden drop in lodgepole pine growth rate in the Delaney and east Cathedral areas beginning in 1950 coincides with the development of outbreak needle miner populations recorded in these areas. The drop was most striking among the young trees and, at the same time, was reflected somewhat earlier than in the mature trees. This is coincident with the observation that the young trees in new infestation areas are more heavily infested at first than the older trees.

The present level of lodgepole pine growth increment in older outbreak areas is barely discernible regardless of tree age. This means a large proportion of stands in these areas will not survive. Even if many trees do survive, including those in the youngest age groups, they may never recover to a normal growth level.

REFERENCES

(1) Martignoni, Mauro E.
1958. Investigations into the possible use of a granulosis virus for the control of the lodgepole needle miner, Recurvaria milleri Busck. 5 pp. (Typewritten).

(2) Morgan, Furness David
1956. Factors influencing the abundance of Recurvaria milleri Busck, (Lepidoptera: Gelechiidae). Thesis Dissertation, Univ. of Calif. 157 pp. (Typewritten)

(3) Patterson, J.E.
1921. Life history of Recurvaria milleri, the lodgepole pine needle miner in Yosemite National Park, California. Jour. of Agr. Res. 21 (3): 127-143, illus.

(4) Peterson, Roger Tory
1941. A field guide to western birds. Houghton Mifflin Company, Boston, 240 pp. illus.

(5) Struble, George R.
1955. Tests of new insecticides to control the lodgepole needle miner. Calif. Forest and Range Exp. Sta., Forest Service, U.S. Dept. of Agric. 8 pp. (Processed).

(6) ________
1955. The lodgepole needle miner in Yosemite National Park, progress report of biological studies in 1954. Calif. Forest and Range Exp. Sta., Forest Service, U.S. Dept. of Agric. 14 pp. illus. (Processed).

(7) ________
1956. Biology and control of the lodgepole needle miner, progress report of 1955 studies. Calif. Forest and Range Exp. Sta., Forest Service, U.S. Dept. of Agric. 29 pp. illus. (Processed).

(8) ________
1957. Biology and control of the lodgepole needle miner, progress report of research in 1956. Calif. Forest and Range Exp. Sta., Forest Service, U.S. Dept. of Agric. 18 pp. (Processed).

(9) Yuill, J.S.
1942. Preliminary studies of the control of the lodgepole needle miner. Jour. Econ. Ent., 35(1): 16-20 illus.

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